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DIFFERENTIAL CAPTURE SUCCESS AND THE INTERSPECIFIC ASSOCIATION OF THE VIRGINIA OPOSSUM (*DIDELPHIS VIRGINIANA*) AND RACCOON (*PROCYON LOTOR*)

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ABSTRACT—Interspecific association plays a key role in the occurrence and abundance of animal populations. Yet, the association of many species is poorly understood, especially with distantly related species such as Virginia opossums (*Didelphis virginiana*) and raccoons (*Procyon lotor*), which have broad niche overlap. Because of the need to better understand the interactions of such species, we assessed the relationship of capture rates of these two species by using live-trap data collected over 6 years of work at the Hobart Ames Plantation and Edward J. Meeman Biological Station in western Tennessee. We found captures of Virginia opossums, raccoons, and both species combined differed across years, but we observed no relationship between the two species. Although water did not need to be within the immediate area of capture for both species, it needed to be close enough for easy access. Raccoons seemed to have no preference of forest type, but Virginia opossums were positively correlated with deciduous forest, which could suggest resource partitioning between the two species. Overall, interactions between the two species suggested a neutral relationship.

RESUMEN—La asociación interespecífica tiene un papel clave en la existencia y abundancia de las poblaciones animales. Sin embargo, tal asociación es poco conocida para muchas especies, especialmente si están lejanamente relacionadas como los tlacuaches nortños (*Didelphis virginiana*) y los mapaches (*Procyon lotor*), que tienen una superposición de nichos muy amplia. Para comprender mejor las interacciones de estas especies, evaluamos la relación de sus tasas de captura en trampas para animales vivos, con datos recopilados durante 6 años de trabajo en la Plantación Hobart Ames y la Estación Biológica Edward J. Meeman en el oeste del estado de Tennessee. Encontramos que las capturas de los tlacuache nortños, de los mapaches y de ambas especies combinadas difirieron a lo largo de los años, pero no observamos ninguna relación entre las dos especies. Asimismo, aunque no es necesario que haya agua dentro del área inmediata de captura para ninguna de las dos especies, es necesario que esté lo suficientemente cerca para facilitar su acceso. Al parecer, los mapaches no tienen preferencia por el tipo de bosque, pero los tlacuaches nortños se correlacionaron positivamente con el bosque caducifolio, lo que podría sugerir una separación de recursos entre las dos especies. En general, las interacciones entre las dos especies sugieren que tienen una relación neutra.

Investigations that are related to the study of co-occurrence of species have been a topic of interest in ecology. Poindexter et al. (2011) pointed out that species co-occurrence was a key area of ecological research and that identification of coexisting taxa is a necessary first step in determining mechanisms enabling habitat sharing. Previous studies have suggested that Virginia opossum (*Didelphis virginiana*) and raccoon (*Procyon lotor*) are interesting models for interspecific-ecological investigations because of their broad niche overlap. For example, similarities are seen in their geographic ranges, activity patterns, food preferences, and habitat use (Kissell and Kennedy, 1992; Gardner and Sunquist, 2003; Gehrt, 2003). Their distributions throughout their geographic ranges are also somewhat similar (McManus, 1974; Lotze and Anderson, 1979).

Virginia opossums and raccoons are nocturnal, omnivorous generalist species that feed on a variety of similar foods (McManus, 1974; Lotze and Anderson, 1979; Gardner, 1982; Symmank et al., 2014; Mims et al., 2022), thereby allowing numerous opportunities for interspecific interactions (see Kissell and Kennedy, 1992; Gardner and Sunquist, 2003; Gehrt, 2003; Symmank et al., 2014; Mims et al., 2022). However, Virginia opossums and raccoons are not closely related taxonomically (Didelphimorphia and Carnivora, respectively). Interactions between such distantly related species are poorly understood.

Virginia opossums and raccoons have been the subject of numerous biological studies involving the capture of each species (McManus, 1974; Lotze and Anderson, 1979; Gardner and Sunquist, 2003; Gehrt, 2003); yet few efforts have been

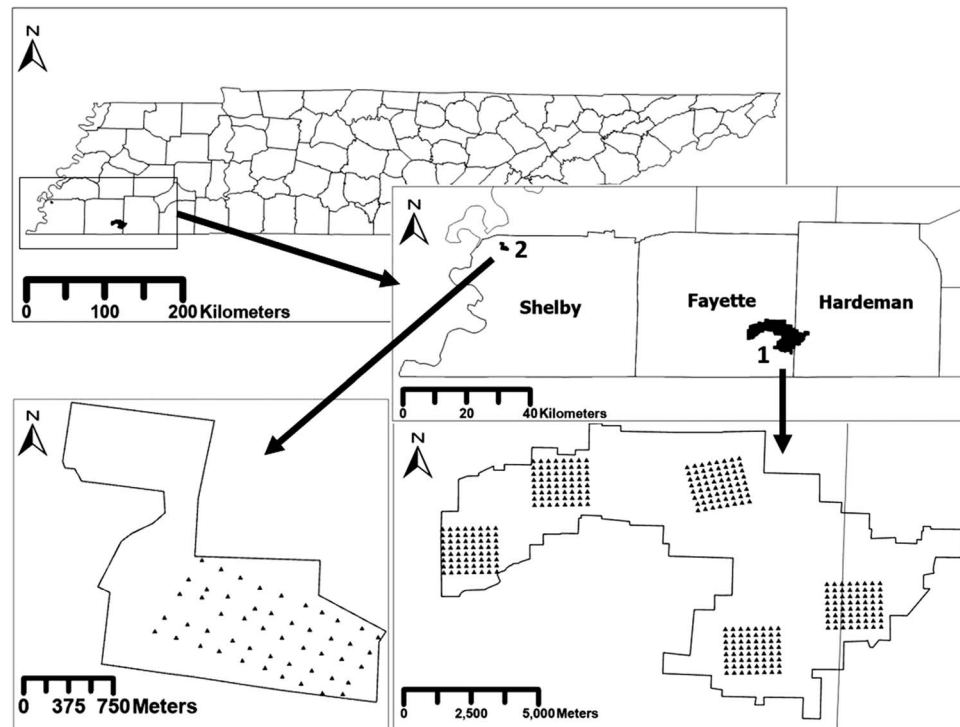


FIG. 1—Study areas for assessment of capture success and interspecific association of the Virginia opossum (*Didelphis virginiana*) and the raccoon (*Procyon lotor*) in western Tennessee, USA: 1) Hobart Ames Plantation, Fayette and Hardeman counties; 2) Edward J. Meeman Biological Station, Shelby Co.

made to investigate the species collectively at the same location. Previous studies have suggested these species demonstrate interspecific competition in sympatry (Ladine, 1997; Ginger et al., 2003), whereas other studies suggest a neutral relationship (Kissell and Kennedy, 1992; Carver, 2009). At present, the issue of differential trap success between these two species across multiple locations as well as the associations of capture success within habitat types and landscape features have not been investigated in detail. Thus, assessing the degree of temporal and spatial association of interspecific interactions could provide novel insight into understanding distributions and habitat utilizations of species and relationships between species and community structure (Cox, 2002). Because of the need for additional insight relating to the interactions between mesopredators and their ecological relationships, we examined the interspecific associations of two of them: Virginia opossum and raccoon. Most previous studies related forested areas and water availability to the presence for both Virginia opossum (Kissell and Kennedy, 1992; Dijak and Thompson, 2000; Baldwin, 2003) and raccoon (Leberg and Kennedy, 1988; Kissell and Kennedy, 1992; Baldwin et al., 2006). Therefore, we hypothesized that higher capture rates for both species would be associated with select habitat features such as forested areas and water availability. Hence, these would be the most suitable areas for studying the interactions of these two species. The purpose of this study was to determine the capture rate of the two species, trapping locations with greatest capture

success for both species, and habitat factors associated with capture success for Virginia opossums and raccoons.

METHODS—Study Area—This study encompassed two sites (Fig. 1) in western Tennessee (TN): Hobart Ames Plantation (Ames) and Edward J. Meeman Biological Station (Meeman). Ames was a rural area used for field research, usually related to agriculture, and consisted of 74.62 km² of both upland and bottomland forest intermixed primarily with agricultural fields and pasture. It was located ca. 5 km northwest of Grand Junction, TN, in Fayette and Hardeman counties. Agricultural crops in the area consisted primarily of soybean (*Glycine max*), corn (*Zea mays*), and cotton (*Gossypium* spp.). Upland forests consisted mainly of loblolly pine (*Pinus taeda*), oaks (*Quercus* spp.), and hickories (*Carya* spp.). Meanwhile, bottomland forests (see Gabor, 1993) were comprised primarily of oaks, maples (*Acer* spp.), cottonwood (*Populus deltoides*), and sweet gum (*Liquidambar styraciflua*).

Meeman was also used for field research, usually ecological studies, and consisted of 2.52 km² of upland and lowland forests, grasslands, and forest edges. The site was located in Shelby Co., TN, approximately 25 km north of Memphis, TN, and 2 km east of the Mississippi River. Upland forests were composed of birches (*Betula* spp.), oaks, and hickories. Lowland forests consisted of mostly elms (*Ulmus* spp.) and cottonwood. Past old fields transitioned into grasslands were throughout the upland areas

and consisted of a mixture of different grasses as well as goldenrod (*Solidago* spp.), blackberry (*Rubus* spp.), and kudzu (*Pueraria lobata*) patches (Maris, 1998).

Data—For this study, we used 6 years (2000–2005) of live-trap data collected during the spring, summer, and winter seasons for Virginia opossums and raccoons collected from Ames and Meeman (see Baldwin, 2003; Carver, 2009; and Wolcott, 2011). Data were from previous live-trapping studies in which Virginia opossums and raccoons were captured using raccoon-sized Tomahawk and Havahart live traps placed in trapping grids (Baldwin et al., 2006). An 8 × 8 trap configuration was used across five trapping grids at Ames, with traps set approximately 230 m apart; at Meeman, a single 5 × 10 trapping grid with traps located approximately 150 m apart was used. Traps were consistently checked and baited every day with approximately 57 g (2 ounces) of canned cat food, canned dog food, and doughnuts as bait across all sites to attract both species. For individual identification, Virginia opossums were tagged in each ear with numbered rabbit tags, and raccoons were tagged in each ear with No. 3 Monel tags (National Band and Tag Co., Newport, Kentucky; see Carver, 2009). For analysis, trap location, date, and species captured were recorded. The total number of operated trap nights (1 trap night = 1 trap set for 1 night) for Ames and Meeman were 73,280 and 19,650, respectively.

Habitat Variables—We used normalized difference vegetation index (NDVI: indicates the density of green, usually vegetation, in the area), slope, elevation, distance to various habitat features (open area, source of open water, river, road, wooded area, and wooded water for both study areas; wooded wetland for Ames only), and habitat type percentages (coniferous forest, cropland, deciduous forest, developed open space, mixed forest, open water, pasture, and shrubland for both study areas; low intensity developed space, medium intensity developed space, herbaceous, herbaceous wetland, and wooded wetland for Ames only). We calculated NDVI in ArcMap 10.5 (Hussainzad and Yusof, 2020) for each year of the study utilizing Landsat imaging collected for each specific year. We also measured distance to habitat features in ArcMap 10.5 with the Euclidean distance tool. To determine habitat-type percentages, we divided each study site into trapping-site cells (for Ames, 230 m by 230 m; for Meeman, 150 m by 150 m) to allow for one trap site within each cell and, within these cells, the area of each habitat type was divided by the total area of that cell.

Data Analyses—We determined the total number of captures (including recaptures) of Virginia opossums, the total number of captures (including recaptures) of raccoons, and the collective number of Virginia opossums plus raccoons captured for each trapping location, each year of trapping, and each trap location per year. Capture success was calculated by dividing the total number of captures by the total number of trap nights similar to Baldwin (2003) and Baldwin et al. (2006). Capture success was calculated for each species and species combined

for each trapping location across all years, all trapping locations collectively for each year of trapping, and each trap location per year. We used a chi-square goodness of fit analysis in SPSS (IBM SPSS Statistics Version 24.0.0.0) to determine if trapping location, trap year, or trap location per year, respectively, had significantly higher than expected capture-success. We used Pearson's correlation coefficient in SPSS to determine the relationship between capture success of the two species and trap location, trap year, and trap location per year, respectively. Also, we used correlation analysis in SPSS to determine relationships between habitat variables and capture success.

RESULTS—Differential Capture Success by Trap Location—Capture rate by trap location for Virginia opossums ranged from 0.00 to 8.54% (mean = $1.45 \pm 1.71\%$ SD) at Ames and 0.00 to 8.40% (mean = $3.69 \pm 1.92\%$ SD) at Meeman. Raccoons had a capture rate by location ranging from 0.00 to 6.10% (mean = $0.95 \pm 1.02\%$ SD) at Ames and 0.00 to 5.86% (mean = $2.89 \pm 1.69\%$ SD) at Meeman. Finally, combined capture rate ranged from 0.00 to 10.37% (mean = $2.40 \pm 2.15\%$ SD) at Ames and 0.01 to 12.47% (mean = $6.03 \pm 2.49\%$ SD) at Meeman. Captures of Virginia opossums (Ames: $\chi^2[319] = 942.71$, $P < 0.001$; Meeman: $\chi^2[49] = 192.17$, $P < 0.001$), raccoons (Ames: $\chi^2[319] = 731.40$, $P < 0.001$; Meeman: $\chi^2[49] = 189.78$, $P < 0.001$), and species combined (Ames: $\chi^2[319] = 1,180.76$, $P < 0.001$; Meeman: $\chi^2[49] = 364.47$, $P < 0.001$) differed across trap sites. We observed a significant positive relationship between raccoons and opossums at Ames ($r = 0.195$, $P < 0.001$), but not at Meeman ($r = -0.05$, $P = 0.748$).

Differential Capture Success by Year—Capture rate by year for Virginia opossums ranged from 0.72 to 2.02% (mean = $1.27 \pm 0.51\%$ SD) at Ames and 1.43 to 5.16% (mean = $3.40 \pm 1.31\%$ SD) at Meeman. Raccoons had a capture rate ranging from 0.44 to 1.65% (mean = $0.98 \pm 0.45\%$ SD) at Ames and 1.43 to 2.90% (mean = $2.29 \pm 0.48\%$ SD) at Meeman. Finally, the capture rate for species combined ranged from 1.29 to 2.93% (mean = $2.25 \pm 0.63\%$ SD) at Ames and 2.87 to 7.41% (mean = $5.69 \pm 1.63\%$ SD) at Meeman. Captures of opossums (Ames: $\chi^2[5] = 2,567.12$, $P < 0.001$; Meeman: $\chi^2[5] = 993.57$, $P < 0.001$), raccoons (Ames: $\chi^2[5] = 1,050.14$, $P < 0.001$; Meeman: $\chi^2[5] = 473.61$, $P = 0.001$), and species combined (Ames: $\chi^2[5] = 2,299.81$, $P < 0.001$; Meeman: $\chi^2[5] = 1456.55$, $P < 0.001$) differed across years; however, we observed no relationship between species either at Ames ($r = -0.155$, $P = 0.770$) or Meeman ($r = 0.57$, $P = 0.234$) indicating that the presence of one had no impact on the other throughout years.

Differential Capture Success by Trap Location per Year—Total trap nights for each year ranged from 4,096 to 19,200 at Ames and 2,000 to 4,500 at Meeman. For most years at each site, we observed a significant difference in capture success among trap locations per year for Virginia opossums, raccoons, and species combined (Table 1). For 2000 at Ames, there was no significant difference in capture success

TABLE 1—Chi-square results of a comparison of capture success among trap locations per year for Virginia opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), and species combined at the Hobart Ames Plantation (= Ames), Fayette and Hardeman counties, Tennessee, and at the Edward J. Meeman Biological Station (= Meeman), Shelby Co., Tennessee. * = significant at the 0.05 level (2-tailed test); ** = significant at the 0.01 level (2-tailed test).

Year	Site	Total trap nights	Virginia opossum		Raccoon		Species combined	
			χ^2	P	χ^2	P	χ^2	P
2000	Ames	4,672	221.60	0.064	194.80	0.410	223.18	0.055
	Meeman	2,650	83.05**	0.002	77.79**	0.005	78.57**	0.005
2001	Ames	18,688	397.31**	0.003	417.57**	<0.001	480.48**	<0.001
	Meeman	4,500	103.72**	<0.001	73.11*	0.014	83.05**	0.002
2002	Ames	14,336	367.22*	0.032	444.84**	<0.001	444.62**	<0.001
	Meeman	4,400	103.18**	<0.001	71.20*	0.021	88.42**	<0.001
2003	Ames	19,200	494.63**	<0.001	307.02	0.675	543.09**	<0.001
	Meeman	4,100	76.00**	0.008	74.70**	0.010	104.42**	<0.001
2004	Ames	12,288	422.07**	<0.001	269.33	0.980	445.97**	<0.001
	Meeman	2,000	103.19**	<0.001	94.49**	<0.001	94.86**	<0.001
2005	Ames	4,096	178.25**	0.002	168.00*	0.009	201.03**	<0.001
	Meeman	2,000	48.02	0.513	72.83*	0.015	56.05	0.227

among trap sites for Virginia opossums, raccoons, or species combined. We observed a significant positive relationship between species at the Ames location for 2002 ($r = 0.16$, $P < 0.01$) and 2004 ($r = 0.14$, $P = 0.02$) as well as between species at the Meeman study site for 2003 ($r = 0.39$, $P < 0.01$), but we did not observe a significant relationship between species for any of the other years at either location.

Comparison of Study Areas—Total trap nights across study areas was 92,930 nights. Capture rate at Ames for Virginia opossums was 1.33%, whereas capture success for raccoons was 0.99%, and capture success of species combined was 2.32%. Capture rates at Meeman were 3.70% for Virginia opossums, 2.34% for raccoons, and 6.04% for species combined. We did not observe a significant difference in capture success between the two study areas for Virginia opossums ($\chi^2 = 0.01$, $CV_{0.05} = 3.84$), raccoons ($\chi^2 = 0.01$, $CV_{0.05} = 3.84$), and species combined ($\chi^2 = 0.02$, $CV_{0.05} = 3.84$). Additionally, we did not observe a significant relationship between study areas based upon year for Virginia opossum ($r = -0.17$, $P = 0.74$), raccoon ($r = -0.61$, $P = 0.20$), and species combined ($r = -0.27$, $P = 0.61$), which indicated that species presence within each year was not related to each other across different study areas.

Correlation of Capture Success and Habitat Features—At Ames, capture success and habitat variables had varying levels of significance among years (Table 2). Habitat variables with more frequent significant positive correlations with differential capture success of Virginia opossums include elevation, distance to nearest road, and percentage herbaceous wetland area. Habitat variables with more frequent significant negative correlations with differential capture success of Virginia opossums include distance to nearest source of open water, distance to nearest wooded area, distance to nearest wooded wetland, percentage coniferous forest, and percentage mixed forest. Habitat variables showing significant positive correlations with differential capture

success of raccoons include percentage herbaceous area, percentage herbaceous wetland area, and percentage open water. Habitat variables with more frequent significant negative correlations with differential capture success of raccoons include distance to nearest river, distance to nearest wooded area, distance to nearest wooded water, and distance to nearest wooded wetland. Some habitat variables (elevation, distance to nearest source of open water, distance to nearest open area, and percentage cropland) exhibited both significantly positive and significantly negative correlations with differential capture success of raccoons creating conflicting relationships.

At Meeman (Table 3), there was only one significant positive correlation between habitat variables and differential capture success of Virginia opossums (distance to nearest open area). Significant negative correlations between habitat variables and differential capture success of Virginia opossums include distance to nearest open source of water, distance to nearest river, distance to nearest road, distance to nearest wooded water, and percentage pasture. Distance to open area also was the only habitat variable that exhibited a significant positive correlation with differential capture success of raccoons. Habitat variables with more frequent significant negative correlations with differential capture success of raccoons include distance to nearest road and percentage pasture.

DISCUSSION—There are several factors that play a role in interspecific associations. It is important to study sympatric species for long periods of time to gain a better understanding of what factors have more importance in community structure. This study entailed vigorous trapping over a 6-year period resulting in a large dataset including tens of thousands of trap nights collectively. The Ames location had a higher sampling effort producing more captures because it was a much bigger area than the Meeman study

TABLE 2—Significant Pearson's correlation coefficients (r) comparing habitat variables and differential capture success of Virginia opossums (*Didelphis virginiana*) and raccoons (*Procyon lotor*) at the Hobart Ames Plantation, Fayette and Hardeman counties, Tennessee. NDVI = normalized difference vegetation index.

Habitat variable	Virginia opossum				Raccoon			
	Year	r	P	n	Year	r	P	n
NDVI	2003	-0.125	0.025	320				
	All	-0.186	0.001	320	All	-0.158	0.005	320
Slope	2002	-0.145	0.009	320				
Elevation	2001	0.190	0.001	320	2001	-0.162	0.004	320
	2002	0.363	<0.001	320	2002	0.121	0.031	320
	2004	0.333	<0.001	320				
	All	0.330	<0.001	320				
Distance to nearest open area					2000	-0.224	0.002	192
					2002	-0.113	0.044	320
	2004	-0.132	0.018	320	2004	0.167	0.003	320
Distance to nearest river					2001	-0.116	0.039	320
					2002	-0.115	0.039	320
					2003	-0.152	0.007	320
					All	-0.150	0.007	320
Distance to nearest source of open water	2001	-0.159	0.004	320				
	2002	-0.205	<0.001	320	2002	-0.168	0.003	320
	2003	-0.169	0.002	320				
	2004	-0.206	<0.001	320				
	All	-0.253	<0.001	320	2005	0.213	0.016	128
Distance to nearest wooded area					2001	-0.170	0.002	320
	2003	-0.206	<0.001	320	2003	-0.207	<0.001	320
	2004	-0.125	0.026	320	2004	-0.123	0.028	320
	All	-0.169	0.002	320	All	-0.204	<0.001	320
Distance to nearest road					2000	-0.265	<0.001	192
	2002	0.136	0.015	320				
	2003	0.132	0.018	320				
	All	0.173	0.002	320				
Distance to nearest wooded wetland					2001	-0.170	0.002	320
	2003	-0.206	<0.001	320	2003	-0.207	<0.001	320
	2004	-0.125	0.026	320	2004	-0.123	0.028	320
	All	-0.169	0.002	320	All	-0.204	<0.001	320
Distance to nearest wooded water					2001	-0.115	0.040	320
					2002	-0.116	0.039	320
					2003	-0.153	0.006	320
					All	-0.151	0.007	320
Percentage coniferous forest	2001	-0.118	0.034	320				
	2002	-0.140	0.012	320				
	2003	-0.180	0.001	320				
	All	-0.160	0.004	320				
Percentage cropland	2002	0.143	0.011	320	2002	0.117	0.036	320
					2003	-0.119	0.034	320
	2004	0.213	<0.001	320				
Percentage deciduous forest	2003	0.146	0.009	320				
Percentage low intensity developed space	2002	0.130	0.020	320				
	All	0.112	0.046	320				
Percentage herbaceous wetland area	2000	0.177	0.014	192				
	2001	0.468	<0.001	320				
	2002	0.169	0.002	320				
	All	0.226	<0.001	320	2004	0.231	<0.001	320

TABLE 2—Continued.

Habitat variable	Virginia opossum				Raccoon			
	Year	<i>r</i>	<i>P</i>	<i>n</i>	Year	<i>r</i>	<i>P</i>	<i>n</i>
Percentage mixed forest	2000	−0.162	0.025	192	2005	0.188	0.034	320
	2002	−0.193	0.001	320				
	All	−0.183	0.001	320				
Percentage herbaceous area	2000	0.142	0.050	192	2002	0.127	0.023	320
Percentage open water								
Percentage shrubland								
Percentage woody wetlands	2003	−0.163	0.004	320				
	2003	0.178	0.001	320				

site. However, overall capture success was not significantly different between the two sites. Given the substantial amount of data given, profound insights into the relationship between these two species can be derived. Our results from capture rates suggest some overlap of desirable conditions for both species. Studies of Virginia opossums and raccoons have found discrepancies in the association of the two species. For example, temporal partitioning has been noted in some studies (Ladine, 1997) but not in others (Carver et al., 2011). Other studies have suggested competition between these two species (Ginger et al., 2003). Overall, our findings displayed a neutral and sometimes positive relationship between capture rates of Virginia opossums and raccoons, which is similar to results observed by Kissell and Kennedy (1992) and Carver (2009). Most spatio-temporal

analyses exhibited neutral relationships except 2 (2002, 2004) of 6 years at Ames and 1 (2003) of 6 years at Meeman. All instances of significant relationships for both study areas displayed positive correlations between capture rates for Virginia opossums and raccoon. Also, capture rates for the two species were not related among years. A year with high capture success for Virginia opossums did not mean high capture success also was observed for raccoons that year. This could mean that climatic factors such as rainfall or temperature may not have a differential impact on capture rates for the presence of both species but could have an impact on one species and not the other. At Ames, a significant positive correlation was noted spatially between capture-success of Virginia opossum and raccoon. Carver (2009) examined the possibility that population sizes may affect species interactions

TABLE 3—Significant Pearson's correlation coefficients (*r*) comparing habitat variables and differential capture success of Virginia opossums (*Didelphis virginiana*) and raccoons (*Procyon lotor*) at the Edward J. Meeman Biological Station, Shelby Co., Tennessee. NDVI = normalized difference vegetation index.

Habitat variable	Virginia opossum				Raccoon			
	Year	<i>r</i>	<i>P</i>	<i>n</i>	Year	<i>r</i>	<i>P</i>	<i>n</i>
NDVI					2000	−0.322	0.023	50
Distance to nearest open area	2000	0.330	0.019	50	2001	0.426	0.002	50
	2001	0.426	0.002	50	2003	0.450	0.001	50
					All	0.388	0.005	50
Distance to nearest open source of water	2000	−0.292	0.040	50	2001	−0.356	0.011	50
	2001	−0.356	0.011	50	All	−0.425	0.002	50
Distance to nearest river	2000	−0.550	<0.001	50	2000	−0.342	0.015	50
					All	−0.353	0.012	50
Distance to nearest road	2000	−0.384	0.006	50	2000	−0.354	0.012	50
					2002	−0.525	<0.001	50
					2003	−0.371	0.008	50
	2005	−0.385	0.006	50				
Distance to nearest wooded water	2000	−0.539	<0.001	50	2000	−0.332	0.019	50
					All	−0.349	0.013	50
Percentage pasture	2001	−0.316	0.025	50	2001	−0.316	0.025	50
	2003	−0.281	0.048	50	2003	−0.326	0.021	50
					All	−0.281	0.048	50

and interpreted any significant correlation between the two as being coincidental and more likely due to varying habitat conditions. However, we observed a neutral relationship between capture-success of these two species at Meeman. Ames is a much larger area with a larger variety of habitat types. If a study area is more uniform in habitat, the distribution of populations will not be as clustered as would be seen in areas with a variety of habitats across the landscape (Gabor, 1993).

Within our study, Virginia opossums were associated with areas that were close to woods. Forested areas have been related to occurrence of Virginia opossums (Kissell and Kennedy, 1992; Dijak and Thompson, 2000; Baldwin, 2003) and raccoons (Leberg and Kennedy, 1988; Kissell and Kennedy, 1992; Baldwin et al., 2006; Chamberlain et al., 2006). Within the present study, Virginia opossums were found more often in areas of deciduous forest rather than in coniferous or mixed forest. This is similar to findings in the Cross Timbers Experimental Range of Oklahoma (Ginger et al., 2003). Conversely, in the Georgia piedmont, most dens of the Virginia opossum were found in upland pine forests (Allen et al., 1985). McKeever (1959) mentioned that Virginia opossums were found in coniferous forests while raccoons were found in upland hardwoods. However, our findings showed that raccoons had no preference on types of forests. The correlation of Virginia opossums with deciduous forest could allude to some resource partitioning between the two species, which could explain why these two species can coexist in the area and align with the niche theory. According to the niche theory, because raccoons and opossums are syntopic species that exhibit high resource overlap, resource partitioning of some sort is necessary for survival (Gause, 1932; Hardin, 1960).

For Virginia opossums, both sites showed higher capture success in areas that were closer to water or areas with high percentages of wooded and herbaceous wetlands. Previous studies have found that presence of this species was related to distance to water (Allen et al., 1985; Levesque, 2001). Also, raccoons were associated with areas that were closer to water sources or areas that were related to high percentages of open water. Baldwin (2003) found that distance to permanent water sources was correlated with raccoon presence, and, in Mississippi, raccoon core-use areas were found close to streams probably in relation to foraging opportunities (Chamberlain et al., 2006). However, there were conflicting results among years with distance to open water which suggests that water in wooded areas may have more of an impact on raccoon presence than open water within our study. Previous research showed some evidence that raccoon presence and areas associated with water are not related (Ginger et al., 2003). The present study found that water on site was not associated with capture success. However, distance to water was negatively associated with both species. Therefore, it seems that water does not need to be present on the site, but sources of water must be available to the species within a certain distance from that

location. The habitat variables used during this study were measured remotely, so nonpermanent sources of water may not have been found with these measurements within the area of the capture sites. Therefore, this study could have overlooked the importance of water in relation to the presence of either species. To gain better insight on the habitat that is associated with the study areas, researchers could incorporate habitat variables measured at the site as well as the remotely measured variables derived for this study.

Virginia opossums were farther from roads at Ames but closer to roads at Meeman. Raccoons used areas that were closer to roads at both sites. The differences in preference of areas relative to roads could be attributed to many things including human interactions, layout of the roads relative to the trap sites, and traveling needs of the animals. Predators may use roads for traveling faster, while expending less energy, and, for some mesopredators including raccoons, the use of roads also could differ based upon seasonal activities (Frey and Conover, 2006).

At both study sites, Virginia opossums were found farther from open areas and in low percentages of pastured lands. Kocer (2004) found that Virginia opossums avoided pastures. However, among different years, there were conflicting results related to preference of cropland areas by Virginia opossums. This may mean that the percentage of croplands in an area does not really affect the presence of Virginia opossums even though some significant correlations were observed within this study. It also could relate to seasonal differences in habitat preference for Virginia opossums. Wolcott (2011) found that higher success of capture of Virginia opossums was in areas farther from fields because these areas are barren during the winter with little to no food available. The presence of raccoons also was associated with areas that had lower percentages of crops perhaps the same reason.

Other studies have noted that raccoons prefer croplands juxtaposed with woody areas (Johnson, 1970; Pedlar et al., 1997). This could provide better foraging opportunities by feeding on the crops until winter, then switching to available foods in the woody areas. Conflicting results among years for correlation between differential capture success of raccoons and percentage pasture as well as distance to open area lead to the possibility that these habitat variables do not affect capture success of raccoons within our study. Furthermore, Virginia opossums within this study were associated with areas having low percentage herbaceous, shrublands, and vegetation density. Raccoons also were associated with areas having low percentage of shrublands. This is probably because dens and food are usually found in forested areas. Raccoons, unlike Virginia opossums, were associated with areas that had high percentage of herbaceous cover but lower NDVI (lower photosynthetic activity). This could be for faster movement or better visibility.

There are numerous factors that can affect resource selection and space use by raccoons which could cause variations in habitat preferences within different study areas

(Chamberlain et al., 2006). Resource selection by raccoons also varies across seasons (Stuewer, 1943; Johnson, 1970; Byrne and Chamberlain, 2011) which could affect habitat preferences among and within study areas. Therefore, future work could include seasonal differences in habitat preferences of Virginia opossums and raccoons across years as well as comparing seasonal habitat preferences for these species from year to year. Furthermore, researchers could include other study areas with varying landscape profiles to further enhance our understanding of habitat preference for these two species. This also could help provide insight on the ecological needs of these two species and improve our understanding of where they can be found during specific seasons or within specific landscapes. In our study, both species appear to be compatible with a variety of different habitat types. This is typical of habitat generalists, but the use of multiple habitat types makes it difficult to model their habitat preferences (as previously noted by Baldwin, 2003). Understanding which habitat variables are similar in areas of varying capture success will help improve our understanding of where to find these species and help predict their occurrences within the site and throughout larger areas. Latitude has been found as a significant factor related to abundance of the Virginia opossum (Dijak and Thompson, 2000), which was not investigated during the present fine-scaled study. With climate change affecting many habitats, there could be change in distribution of the Virginia opossum which could increase opportunities for interactions with raccoons.

Differences in the association of two species could be attributed to other wildlife in the area that were not factored into our analyses. According to Davidson (1980), if a third species were introduced in an area in which two possible competitors already exist, behavioral changes may arise that cannot be predicted with linear models. There are other mesopredators and predators within the study areas including foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and skunks (*Mephitis mephitis* and *Spilogale putorius*), and their presence may have an impact on the presence of either Virginia opossums or raccoons. Smaller mesopredators may avoid areas that are used by larger mesopredators to alleviate interspecific competition (Fedriani et al., 1999). The impact a larger predator has on species presence may be different among Virginia opossums and raccoons. In Ohio, raccoons had a lower occupancy rate when Virginia opossums were present, but occupancy by Virginia opossums was not affected by raccoon presence; and both species had a weak negative relationship with coyotes (Rich et al., 2018). Population densities of coyotes may be different between Ames and Meeman which could cause differences in the capture rates of raccoons and Virginia opossums between the study areas. Furthermore, a study conducted in California suggested that raccoons may avoid predator hotspots but did not note this for Virginia opossums (Wang et al., 2020). Therefore, the total number

of other predators in general within the area may have more influence on raccoons than would a specific species. Finally, anthropogenic factors such as disturbance and habitat modification also can affect species presence which could affect results related to interspecific interactions in that area. Ames was more rural than Meeman. Possible discrepancies found within our results could be due to differences in landscape and community structure between our study areas. Future work could include a more robust occupancy model to better understand the differences interspecific relationships and capture rates in these two areas. Even though some resource partitioning may have been observed, there was no direct competition observed in the present study. Therefore, it is plausible that predicting the co-occurrence of these two species via species distribution modeling would be possible in future work.

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